

CHEMORECEPTION IN CIRRIPEDES

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In reviewing the different functions of cirral activity in barnacles, Crisp and Southward (1961) distinguished captorial feeding, in which larger food particles were caught in the cirral net, from microphagy, in which small particles were filtered from the water currents entering the mantle cavity.

They found a number of differences between the action of the cirri of the more primitive Thoracica, the stalked barnacles or *Lepadidae*, and that of the most advanced sessile forms, the *Balanidae*. In the *Lepadidae*, as Barnes and Reese (1959) had previously demonstrated with *Pollicipes polymerus*, the cirri sometimes roll up independently and sometimes together, whereas the cirri of the *Balanidae* almost invariably roll up synchronously, enclosing the prey in a compact cirral net. The *Lepadidae* usually rely on external water movements to bring food into the cirral net. They display less specialized forms of cirral activity, extending the cirri passively against the flow of water until food particles are caught.

The *Balanidae* display a greater variety of feeding mechanisms including the active capture of larger prey in the course of rhythmic cirral activity and the filtration of fine particles with the cirral net wholly or partially extended. With certain exceptions, members of the *Lepadidae* are less sensitive to mechanical shock and remain closed afterwards for shorter periods than members of the *Balanidae*.

Crisp and Southward offered evidence that some of the *Balanidae* were able to select between nutritious and non-nutritious particles caught on the extended cirral net. Cellulose fibers, air bubbles, and other inert particles were ignored, but when food particles touched the cirral net, the cirri closed on them and transferred them to the mouth. Food particles were not only ingested to a greater extent, but the presence of food in the water in the form of small plankton or finely chopped muscle tissue appeared to stimulate more active and continuous feeding. This effect was later demonstrated by continuously recording the cirral movements of the barnacle *Elminius modestus* (Southward and Crisp, 1965). An ability to respond to chemical substances dissolved in the surrounding water or diffusing from captured food material impaled on the cirri seems the most likely means by which food is selected on capture. It is interesting to note that in the cinematographic record of the capture of a food particle (Crisp and Southward, 1961; Fig. 14), there was a delay of 0.3–0.5 sec. after the particle had struck the cirrus before the closing action began. Less delay would have been expected for a direct response to a mechanical stimulus than for a response brought about by diffusion of material from the food particle to a receptor.

Barnes and Reese (1959) reached quite different conclusions from observations on the behavior of the stalked barnacle *Pollicipes polymerus*. They found that lightly touching the inner surface of the flagellum of the cirrus with a needle caused

it to flex independently. Stronger or repeated stimuli led to a graded response in which more and more of the cirri bent over the needle, culminating in a typical captorial enclosure by the whole cirral apparatus. They suggested that repeated mechanical stimuli caused by the struggling movements of the prey, like those evoked by the needle, progressively reinforced each other and resulted in capture of the prey and its transfer to the mouth. Such an experiment cannot readily be performed on most balanomorph species because touch so readily elicits a shock reaction. Barnes (1959) observed both organic and inorganic particles in the stomach contents of several different species of acorn barnacles, from which he concluded that there was little selection. Nevertheless he thought a chemotactic sense determined whether particles, after having been manipulated in the oral region, were later swallowed or rejected. From an examination of the stomach contents of *Pollicipes polymorphus* he obtained evidence of selection in favor of animal prey, but he ruled out the likelihood that chemosensation played any part and considered the distinction between living prey and sand particles was entirely mediated by mechanoreceptors.

The experiments described below were carried out to determine whether a purely chemical stimulus can elicit feeding response in cirripedes. Pedunculate forms were used since Barnes formed his views largely as a result of experimenting with one such species.

In this paper the phrase "chemical stimulation" is used to describe movements, apparently concerned with food capture, induced by chemical substances dissolved in the water. The inhibitory or narcotic effect of chemicals causing reduction in cirral activity, though referred to by Cole and Allison (1930, 1932, 1933, 1937) as "chemical stimulation," is not considered relevant to this study.

METHODS

Two species of pedunculate barnacles were used for the majority of investigations, *Lepas anatifera* and *Lepas fascicularis*. The former was found attached to pieces of floating wood, the latter to floating fronds of *Fucus vesiculosus*. *Lepas anatifera* was found to be the more robust and reliable species for experimental work, and quantitative studies were confined to it. Qualitative observations were usually replicated on *Lepas fascicularis* with results closely similar to those found with *L. anatifera*.

The animals were maintained in a large tank of about 50 L. capacity in which the water was kept flowing continuously. They were fed each evening on scraps of *Mytilus edulis*.

Tests for chemosensory behavior were made as follows. About 0.3 ml. of test solution was sucked into an Aglar micro syringe fitted with a fine hypodermic needle and a micrometer screw-driven piston which allowed deliveries of solution to an accuracy of ± 0.0005 cc. to be made without difficulty. The tip of the needle was held about 3 cm. from a selected individual, and directed towards part of its open cirral net, usually about half-way along the flagellum of a cirrus. The exact position seemed unimportant, and similar results were obtained if the needle was directed at the mouth parts. A jet of solution of 0.01 cc. was then squirted on to the cirrus by turning the micrometer head through 360°. The solution was considered to have caused a response if the cirrus rolled up, whether independently

or as part of a general contraction of the cirral apparatus. Typically, a strong stimulus caused the whole set of larger cirri immediately to close over the mouth and to draw themselves several times over the shorter cirri which, meanwhile, executed rapid reciprocating movements as though forcing food towards the oral cone. When a partial closure involving only a few cirri was observed it was designated a weak response.

Whenever positive responses were observed, a control observation was made by squirting 0.01 cc. of sea water over the same animal. Only rarely did this evoke any response, and then only a partial flexure of an individual cirrus, which was not usually repeated when sea water was squirted again. Solutions giving a true feeding reaction, in contrast, gave consistent and repeatable responses, usually by more than a single cirrus.

Failure to produce a response by a given solution was confirmed by squirting at the same individual in place of the solution, a suspension of one part of milk in three parts of sea water; this invariably caused a response.

Quantitative measurements of the threshold of sensitivity were made by serial dilution of the test chemical by a factor of 1.5 or 2 times. At each concentration, some 20 tests were made and the percentage of positive responses counted. The threshold value was taken as the point at which 50% of individuals failed to give the response.

Except where otherwise stated, solutions were made up in laboratory sea water, and tested for neutrality before use.

Observations were originally made on *Lepas anatifera* washed up at Woods Hole. Later, a population washed up on the west coast of Anglesey was tested using glycine, and gave identical results (Fig. 3).

PRELIMINARY EXPERIMENTS

Initially, a number of naturally occurring and pure substances were applied to the cirri to indicate the kind of material likely to be worthy of quantitative investigation. Milk, bacto-peptone, coelomic fluids of animals, and tissue extracts invariably gave rise to strong feeding responses. Solutions of proteins, such as gelatin and pepsin, caused rather weak reactions which became even less definite after dialysis, but several amino acids, such as glycine, alanine, glutamic acid, arginine, proline, and serine, gave a clear positive response, while the peptide, reduced glutathione (at $1.6 \times 10^{-2} M$), and solutions of the larger amino acids gave generally weak feeding reactions. Allantoin failed to give a definite response at all.

Sugars such as sucrose, glucose, galactose and lactose, and cultures of *Phacodactylum* and *Dunaliella* were all without effect; a strong suspension of soluble starch and a solution of glycogen elicited only very weak responses.

Organic substances in general caused no reaction. Sodium acetate and caproate ($1.6 \times 10^{-2} M$), sodium benzoate ($5 \times 10^{-2} M$) and stearate, ethyl alcohol (10%), sea water saturated in aniline, and tetramethylammonium chloride were tested, all with negative results.

Certain substances that altered the pH of sea water through hydrolysis caused an apparent feeding reaction accompanied by a withdrawal movement of the whole animal brought about by bending the stalk. The latter reaction was evident when

strong solutions of aspartic acid and cysteine which were rather far from neutrality were used, and also on application of certain amino acids in neutral solution (see below). Similar stalk-bending reactions, as well as feeding reactions, were observed when sea water was made acid or alkaline and squirted over the animals. The range of pH which did not elicit any response was found to lie between pH 7.5 and 9.5, and any test solutions whose pH did not fall well inside these limits were discarded. Sodium bicarbonate at 0.5 M was found to give satisfactory

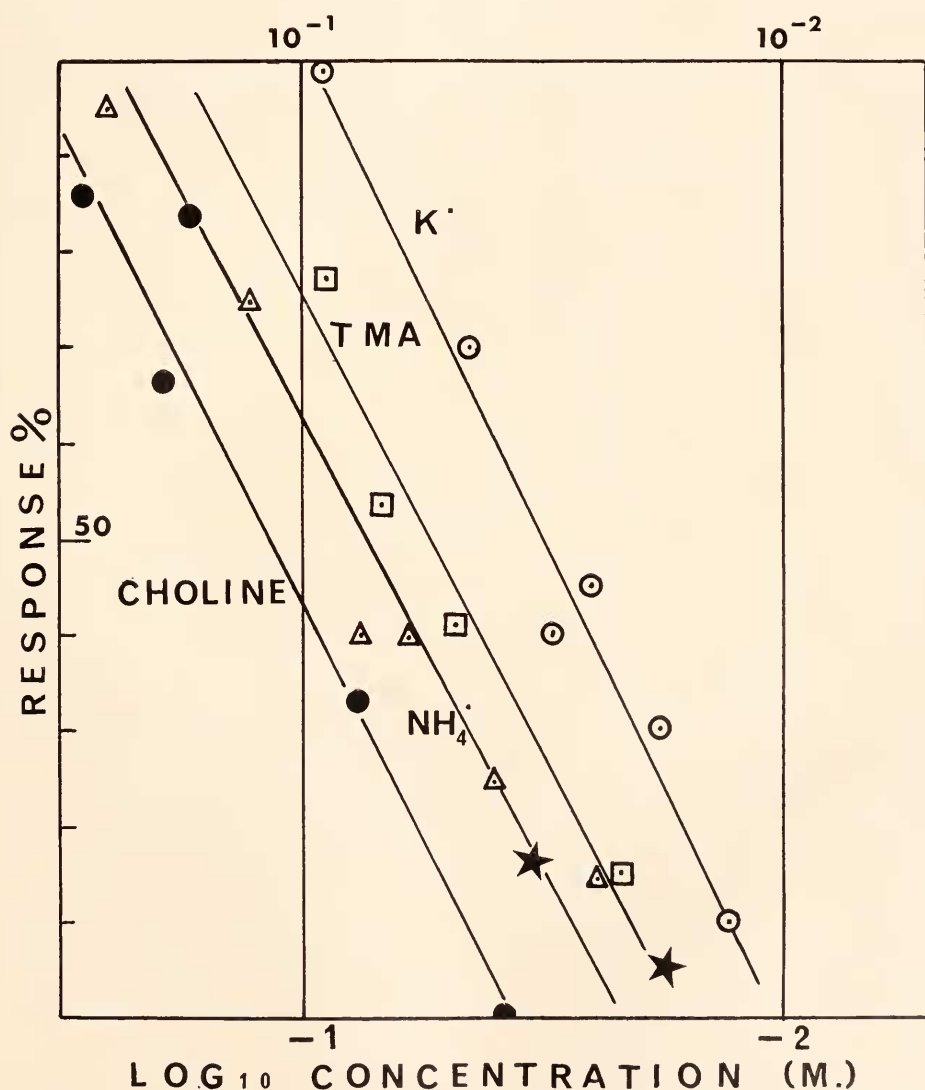


FIGURE 1. Reaction of *Lepas anatifera* to solutions of various cations in neutral solution in sea water, buffered where necessary with carbonate. Potassium: open circles. Trimethylamine: squares. Trimethylamine oxide: stars. Ammonium: triangles. Choline: full circles.

buffering for most of the more acid solutes and did not itself produce any reaction. Distilled water produced a shock reaction, causing the animal to close temporarily, but sea water diluted by 50% had no effect.

RESPONSES TO INORGANIC IONS

In addition to the influence of the hydrogen ion, the effect of solutions of other inorganic cations was tested by mixing solutions of salts with sea water in varying proportions. Of the commoner salts, only those with monovalent cations evoked

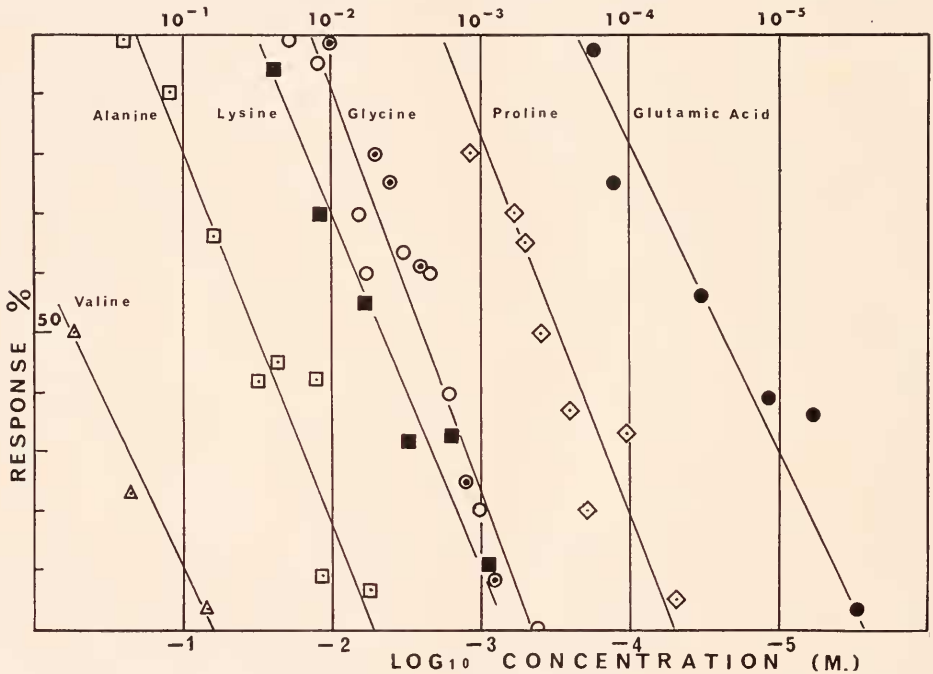


FIGURE 2. Reaction of *Lepas anatifera* to solutions of amino acids in neutral solution in sea water, buffered where necessary with carbonate. L-valine: triangles. L-alanine: open squares. L-glycine, Woods Hole population of *Lepas*: open circles. L-glycine, North Wales population of *Lepas*: ringed circles. L-proline: diamonds. L-lysine: full squares. L-glutamic acid: full circles.

any response, and then only at concentrations exceeding 10^{-2} M. Since the sodium ion is present in such high concentration in sea water, it was not expected to have any effect, and indeed equimolar (0.5 M) solutions of sodium chloride or sodium bicarbonate had none. Hypertonic solutions (1.0 M) of sodium chloride did, however, evoke a regular response. Ammonium salts (chloride, sulfate and nitrate) neutralized with sodium bicarbonate, and potassium salts brought about a feeding reaction at much lower concentrations, as shown in Figure 1. The figure shows that, within the 10 and 90 percentile values of the number of animals responding in the sample population, an approximately linear relationship exists between the

percentage response, and the logarithm of the concentration applied. The concentration at the intercept with a response by 50% of the population is taken to characterize the population threshold for the substance. This was 6.6 and $3.0 \times 10^{-2} M$, respectively, for ammonium and potassium. Calcium, strontium and magnesium had no influence when used at strengths of $0.5 M$. However, when magnesium and potassium ions were present in equal amounts, the effect of the potassium ion was slightly reduced, indicating antagonism. Inorganic anions appeared to be quite ineffective.

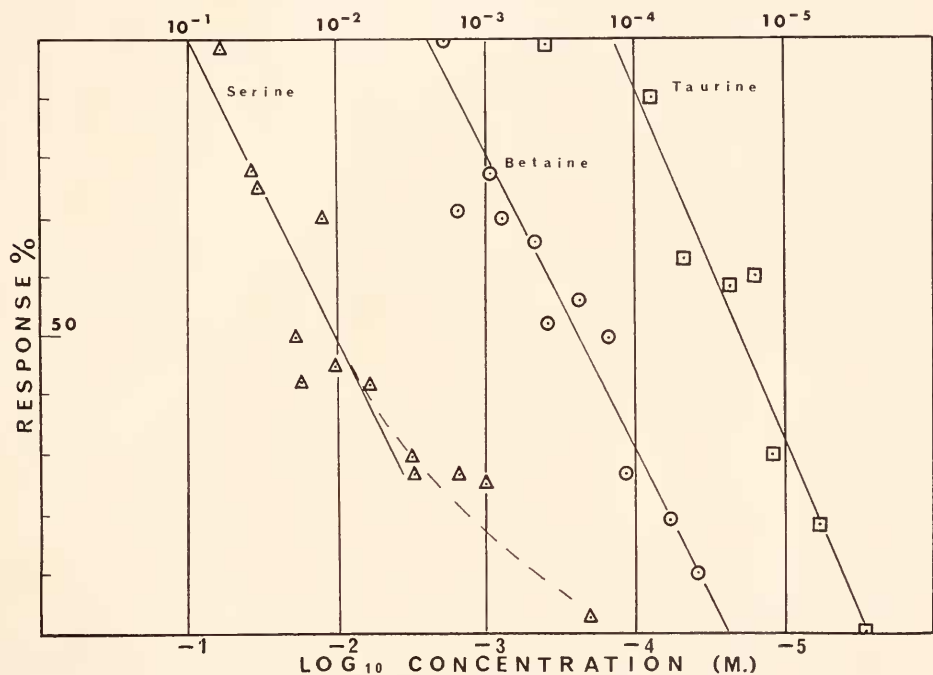


FIGURE 3. Reaction of *Lepas anatifera* to solutions of ampholytes. L-serine: triangles. Betaine: circles. Taurine: squares. The broken line for L-serine indicates predominance of stalk rather than feeding responses in the range of concentration shown (see text).

RESPONSES TO AMINO ACIDS AND RELATED COMPOUNDS

A typical series of results for some amino acids and related compounds, plotted as response against Log concentration, is shown in Figures 2 and 3. The lines are fitted by eye.

The 50% intercepts of these, and of other compounds tested, are listed in Table I. The standard deviation of individual thresholds of response, taken as half the difference in the $\text{Log}_{10}c$ values corresponding to 84% and 16%, respectively, of the population responding, are entered in Table I, Column 4. It will be seen that the standard deviations for all the amino acids in which a sufficient range of response could be evoked, and also those for betaine and taurine, varied little about a mean value of 0.6. The threshold concentrations are thus at least four times

greater ($10^{0.6}$) in the less sensitive 16 percentile of the population and only one-quarter as large in the more sensitive 16 percentile. In reading the Table it is therefore important to remember that some individuals can respond to concentrations much lower than those listed in Column 3.

TABLE 1
*Concentrations of amino acids and related substances required to produce 50% feeding responses by *Lepas anatifera**

Amino acid and molecular wt.	Median limiting concentration for population response (molar)	Standard deviation** of response (Log ₁₀ molarity)	Comments
1. Neutral			
Glycine (75)	2.4×10^{-3}	0.54	
L-Alanine (90)	3.2×10^{-2}	0.58	
L-Valine (117)	5×10^{-1}	0.65	
*L-Leucine (131)	$>1.5 \times 10^{-1}$	—	Weak response
*IsoLeucine (131)	$>1.7 \times 10^{-1}$	—	No effect observed
L-Proline (115)	3.2×10^{-4}	0.54	
L-Phenylalanine (165)	1.4×10^{-2}	0.58	
L-Tryptophan (224)	$>5 \times 10^{-2}$	—	Weak response
L-Serine (105)	1.2×10^{-2}	0.70	Stalk response
L-Tyrosine (181)	2.3×10^{-3}	—	
L-Cysteine (121)	$>7 \times 10^{-1}$	—	No effect observed
*L-Cysteine (240)	$>4 \times 10^{-2}$	—	No effect observed
*L-Methionine (149)	$>2 \times 10^{-2}$	—	No effect observed
L-Asparagine (132)	$>3 \times 10^{-1}$	—	Stalk response, weak feeding response
2. Acidic			
L-Aspartic acid (133)	3×10^{-2}	0.60	
L-Glutamic acid (147)	2.5×10^{-5}	0.68	
3. Basic			
L-Lysine (146)	4.5×10^{-3}	0.60	
L-Arginine (174)	3×10^{-3}	0.62	
L-Histidine (155)	$>6 \times 10^{-2}$	—	Stalk response, weak feeding response
4. Related Compounds			
Betaine (117)	2.4×10^{-4}	0.70	
Taurine (125)	2.0×10^{-5}	0.63	

* Concentration limited by poor solubility.

** The standard deviation given is half the change in Log₁₀ concentration, between a 16% and an 84% response by the sample population.

There are great differences in capacity to evoke a feeding response between the compounds listed. L-glutamic acid and taurine are outstandingly stimulating, concentrations of the order of 10^{-5} M being sufficient (Fig. 2). Betaine and L-proline are also very effective, evoking reactions at 10^{-4} M. Four naturally occurring amino acids stimulate at about 10^{-3} M: L-glycine, L-tyrosine, L-lysine and L-

arginine; four at 10^{-2} M: L- α alanine, L-phenyl alanine, L-serine and L-aspartic acid; five stimulate only weakly at high concentration: L-valine, L-leucine, L-tryptophan, L-histidine and L-asparagine; while L-isoleucine and the sulfur-containing amino acids L-cysteine, L-cystine and L-methionine, are without effect. The stimulating capacity of some amino acids was clearly limited by low solubility, for example, L-valine (Fig. 2). Perhaps isoleucine, cystine and methionine would have had some effect if more concentrated solutions had been possible.

RESPONSES TO ORGANIC CATIONS

Five organic cations were tested, using solutions buffered to pH 8: trimethylamine, trimethylamine oxide, triethylamine, choline, and putrescine. The results are included in Table II. Only choline and trimethylamine gave measurable responses, but the concentration required was greater than that for potassium and

TABLE II
Concentrations of organic and inorganic cations required to produce 50% feeding response in Lepas anatifera

Cation	Ionic mass	Limiting concentration (molar)	Standard* deviation	Comments
Potassium	39	3.1×10^{-2}	0.31	Very slight response Slight response
Ammonium	18	6.6×10^{-2}	0.38	
Trimethylamine	60	5.4×10^{-2}	0.36	
Triethylamine	102	$>1 \times 10^{-1}$	—	
Trimethylamine oxide	76	$>4 \times 10^{-2}$	—	
Choline	104	1.1×10^{-1}	0.36	No response
Putrescine	89	$>5 \times 10^{-1}$	—	

* See footnote Table 1.

ammonium. The response to cations was more uniform than that to amino acids, as can be seen from the values of standard deviation, which approximate to half those for the amino acids.

STALK RESPONSES

Three of the amino acids regularly caused slow bending movements of the stalk. When applied at high concentration, L-serine produced an immediate feeding response, usually followed by a stalk reaction a second or two later; sometimes the stalk movements continued for some 5 to 10 seconds and the animal usually remained in the new position it had assumed for much longer periods. When L-serine was applied at concentrations too low to initiate feeding, stalk movements sometimes followed after a few seconds' delay. The response curve for this compound was also anomalous (Fig. 3). L-histidine and L-asparagine among the amino acids gave inconclusive results when tested for feeding reactions, only a proportion of the individuals showing typical responses. Feeding responses were given at a range of concentrations down to about 10^{-2} M by histidine but stalk responses, after the usual long delay, occurred down to concentrations of 3×10^{-3} M. Histidine could also induce almost closed individuals to open the valves and

display the cirri. L-asparagine similarly failed to produce positive and regular feeding responses by the cirri and mouth parts but, like histidine, caused delayed stalk responses when applied to the cirri at concentrations of 10^{-1} M which were subliminal for the feeding response. Stalk responses were also noticed when strongly acid or alkaline solutions were applied.

Usually the direction of the movement during a stalk response suggests withdrawal from an unfavorable stimulus; the cirral net moves away from the source of water entering the net (*i.e.* in the sense from rostrum to carina) and weaves slowly from side to side. However, though valve closure would be expected to accompany any reaction to unfavorable stimuli, the valves do not close; in fact, in the case of histidine, they open more widely. The idea of an avoidance response is also inconsistent with the long latency of the reaction, and the fact that it can be produced by concentrations of stimulating substance below those causing feeding responses. Further investigation is required to establish its significance.

CHEMORECEPTION IN SESSILE BARNACLES

A few qualitative experiments were made with *Balanus balanoides* and *Elminius modestus* which indicated that feeding activity was stimulated by amino acids at concentrations similar to those used in experiments with *Lepas*. Unfortunately, quantitative methods are more difficult to apply to balanids. They are much more prone to close when shadows are cast on them or when mechanical shocks are applied, and feeding movements are less readily distinguishable from ordinary cirral movements. The turtle barnacle *Platylepas bissexlobata*, like other epizoic forms, is less responsive to shock, and showed very clear feeding responses. It reacted to glutamic acid at concentrations between 10^{-4} and 10^{-5} M, and to potassium ions, but not to sugars and other organic substances.

It is reasonable therefore to conclude that the results of experiments on *Lepas* typify the behavior of the majority of cirripedes.

DISCUSSION

The cirri and mouth parts of *Lepas* and probably of the majority of cirripedes are sensitive to two groups of substances: certain of the amino acids and related compounds taurine and betaine on the one hand, and certain cations of the other, notably potassium, choline, and trimethylamine. High concentrations of hydrogen and hydroxyl ions represent conditions unlikely to be experienced in nature, and the animals' response is probably a shock reaction rather than a true feeding response. No responses were elicited by neutral organic molecules, such as alcohols and sugars, nor by anions, whether organic or inorganic, other than glutamate and aspartate.

The two groups of compounds producing feeding reactions in *Lepas* are similar to those that influence feeding and food orientation in many marine carnivores—ctenophores, molluscs, polychaetes, and other Crustacea (Case and Gwilliam, 1963). Electrophysiological studies on higher Crustacea have similarly revealed sensory units receptive to amino acids and tertiary amines. Laverack (1963a, 1963b), using rather high concentrations of trimethylamine (10^{-1} M) and other substances containing the group $N(CH_3)_3$, found three types of receptors on the crab dactylo-

podite which responded to these substances but not to amino acids. Case and Gwilliam (1961) had been able to record from the same preparation units highly sensitive to the L-isomer of glutamic acid and to a lesser degree to some of its derivatives and to other amino acids. Levandowsky and Hodgson (1965) found in preparations of dactylopodite and antennule of *Palinurus argos* evidence for separate units, some sensitive to L-glutamic acid in very low concentration (10^{-4} M) and others to tertiary amines (10^{-3} M). Hodgson (1958) reported that the antennules and chelae of the fresh-water crustacean *Cambarus* responded well to glutamic acid at very high concentration (0.25 M), rather less well to glycine and glutamine, and not at all to a variety of other substances. Similarly, Case, Gwilliam and Hanson (1960), using dactylopodite receptors of the crabs *Libinia emarginata*, *Callinectes sapidus* and *Carcinides maenas*, obtained positive results for all amino acids tested, with greatest sensitivity to glutamic acid, but no response to alcohols (0.2 M), monosaccharides (0.25 M), or peptides, including glutathione. The coxal gnathobases, walking legs, and chilidia of the marine arachnid *Limulus* also are sensitive to amino acids but, unlike the Crustacea so far investigated, glycine, not glutamic acid, elicited the strongest response (Barber and Hayes, 1963).

Barnacles therefore resemble other crustaceans in their ability to respond to many amino acids at low concentrations (10^{-2} to 10^{-5} M, Table I), and to cations, such as tertiary amines, at rather higher concentrations (10^{-1} to 10^{-2} M, Table II). The sensitivity range, as shown by the standard deviation (Tables I and II), was quite different for the two classes of compounds, suggesting different receptor mechanisms as in crabs (Laverack, 1963a, 1963b) and in *Palinurus* (Levandowsky and Hodgson, 1965).

The outstanding and specific sensitivity of the chemoreceptors of *Lepas* and of other Crustacea to low concentrations of L-glutamic acid, a physiologically active compound suspected as a neural transmitter in arthropods (Takeuchi and Takeuchi, 1964), and to substances closely related to neural transmitters, such as betaine and choline, raises the question whether this is a normal gustatory response. Although glutamate was effective at a concentration of only 10^{-5} M in the medium external to the sense organ, it is known that concentrations as low as 10^{-10} g./ml. will stimulate *Helix* neurones when directly applied (Kerkut and Walker, 1961). However, not only did glutamate produce a response which resembled normal feeding, but some other substances, not regarded as having a special physiological role, were also able to produce a feeding reaction in *Lepas* at low concentrations, for example L-proline and taurine.

Moreover, although there is a general similarity in the classes of compounds to which marine arthropods respond and a particular sensitivity to L-glutamic acid, the order of sensitivity to different compounds is not always the same for different species, but differs as one might expect of gustatory or olfactory responses. Thus in *Lepas*, proline is the most effective amino acid after glutamic acid, while the peptides ornithine and reduced glutathione are non-stimulatory. On the other hand in *Carcinides*, ornithine has more effect than proline and reduced glutathione also causes a response. Taurine and glutamic acid are the most effective stimuli to *Lepas*, but have only weak effects on the chemoreceptors of *Limulus*. Indeed, if a comparison be made between *Lepas* and *Carcinides*, two crustaceans on which

a number of compounds have been tested quantitatively, there is little correlation in the sensitivity ranking of compounds between the two species, and no correlation between sensitivity and any obvious physical or chemical property. There is no general relationship to molecular weight or volume (though peptides and proteins are usually ineffective compared with amino acids), and no relationship to ionization constants or to specific groupings. All that can be said in general is that the most strongly stimulating substances are ampholytes, existing in solution as zwitterions, and that sugars and other neutral substances are wholly ignored.

Some of the substances to which Crustacea are sensitive may afford reliable and efficient guides to the presence of food; scavenging crabs and lobsters would be expected to respond to tertiary amines and betaines present in decaying animal tissue (Laverack, 1963b) as well as to amino acids released by autolysis. But there is no reason to suppose that glutamic acid and taurine, widely distributed as they are (Simpson *et al.* 1959), have any special claim to serve as feeding-inducing substances in the place of other and more commonly occurring amino acids which would also be released. Dr. D. A. Dorsett pointed out to me in this connection that there are many examples in man of strong olfactory and gustatory responses to chemicals which have no adaptive significance. One should not therefore expect that the substances most relevant to the animals' needs will necessarily produce the strongest feeding responses. Crustacean sense organs may just happen to be very sensitive to such substances as glutamic acid but, in suitable circumstances, this high degree of sensitivity might be made to function as a clue to the presence of food.

The responses to amino acids by *Lepas* are at first sight difficult to explain on the basis of food searching and recognition, since the animal is sessile and unlikely often to come into contact with decaying material. However, its food normally consists of living plankton, and there is some evidence that amino acids may diffuse from planktonic animals (Webb and Johannes, 1965). In any case, since the cirri of barnacles are beset with sharp spines, a delicate organism might be pierced on contact with the cirral net, and would very likely be crushed as the flagellum of the cirrus curled around it. If, as a result, stimulating substances were released, a feeding response would reinforce any initial mechanical stimulus, and cause living prey to be devoured. We do not know the composition of the body fluids of planktonic larvae, but if they resemble those of the adults they will often contain amino acids. *Asterias* body fluid evokes a strong feeding response in *Lepas*. Furthermore, although the body fluids may not differ greatly from oceanic water in their concentration of potassium ($1 \times 10^{-2} M$; Dittmar, 1884), the intracellular fluids of animals contain much higher concentrations, often as much as ten times that of sea water (see Prosser and Brown, 1961). Release of potassium sufficient to raise the local concentration to twice that of sea water is evidently sufficient to evoke a feeding response (Table II). The sensitivity of *Lepas* to potassium ions may therefore have some adaptive value in reinforcing the feeding reaction when live prey is caught.

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SUMMARY

1. Feeding responses were elicited when solutions of amino acids and of organic and inorganic cations were applied to the cirri and mouth parts of *Lepas* and other barnacles. Proteins, peptides, sugars, neutral organic molecules, and anions were without effect.

2. Of the common amino acids, *Lepas anatifera* was most responsive to L-glutamic acid and L-proline. It was very sensitive also to betaine and taurine.

3. The order of sensitivity to amino acids and to other zwitterionic substances did not correlate with any obvious physical or chemical property.

4. Inorganic and organic cations had to be applied at higher concentrations than many amino acids to produce a response and probably acted on different receptors. The potassium ion had the greatest effect of those tested.

5. The observed sensitivity to amino acids and to potassium ions is thought to enable the animal to recognize living prey after it has been pierced by the setae present on the cirri.

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